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PHYSIOLOGY OF THE WOOD BORING MOLLUSC *MARTESIA CUNEIFORMIS* SAY

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Abstract

Larvae of *Martesia cuneiformis* Say settled in greatest abundance (151.5 individuals/square meter surface area of wood substrate) during the months of August, September, and October in a North Carolina estuary. Minimum estimates of post settlement shell growth rates are 0.19 mm/day during the summer months and 0.03 mm/day during the winter months. Gravid adults maintained in the laboratory spawn during physical disturbance of dissection from wood and, in isolated individuals, after thermal stimulation. The first shelled veliger larva has a mean shell size of 69.0 μm long and 60.0 μm high. At 22°C and 30–32‰ salinity the pediveliger stage, with a mean shell size of 260 μm long and 269 μm high, is reached in 35 days. Larval respiration rate is described by the relationship $R = 2.22W^{2.42}$ where R is oxygen consumption (nl O_2/larva/h) and W is dry weight (μg). On starvation larvae predominantly utilize protein and lipid as respiratory substrates. Adult respiration and ammonia excretion rates are described by the relationships $R = 17.95W^{0.703}$ and $E = 0.133W^{0.492}$ respectively with the units R (μl O_2/individual/h), E (μg at NH_3-N/individual/h), and W (g live weight).

Introduction

Bivalve molluscs of the family Pholadidae are unusual in that, in the adult form, they bore into a variety of substrates including sand, peat, clay, wood, calcareous shells of other molluscs, and rocks varying in hardness from sandstone and limestone to chert and shale. Certain aspects of the biology of the Pholadidae are reasonably well documented. They have a bathymetric range varying from the intertidal and shallow subtidal (Turner, 1954) to opportunistic occurrence in woody substrates in the deep sea (subfamily Xylophagainae, see Turner, 1973). The taxonomy of the members of the family has received considerable attention (Turner 1954, 1955) and remains a subject of active research. The larvae of a number of species have also been cultured and described (Lebour, 1938; Werner, 1939; Jorgensen, 1946; Rees, 1950; Chanley, 1965; Chanley and Andrews, 1971; Boyle and Turner, 1976). By contrast data on the physiology of both the larval and adult forms, with exception of work on adult *Martesia fragilis* (Verrill and Bush) and in one instance *Martesia striata* Linné (Nagabushnam, 1961; Srinivasan, 1961, 1962, 1963a, b, c; Srinivasan and Krishnaswamy, 1964) are rare.

As part of a larger study of bioenergetics of wood boring molluscs of the family Teredinidae the opportunity arose to collect adult pholads, *Martesia cuneiformis* Say. This report describes subsequent studies in which these adults were maintained and induced to spawn in the laboratory. The larvae were cultured to metamorphosis and used to examine aspects of respiration and change in biochemical composition during

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growth and starvation. The relationship of oxygen consumption to nitrogenous excretion of adult animals was also examined.

Materials and Methods

Seasonality of settlement for *Martesia cuneiformis* larvae was determined for the Beaufort, North Carolina region by suspending fir panels ($15 \times 9 \times 4$ cm = 0.462 m^2) below mean low water off the dock of the Duke University Marine Laboratory. Ten groups of 10–12 panels each were immersed for varying lengths of time (2–6 months) over a three year period. On retrieval panels were cleaned of attached macrofauna, wrapped in wet paper, packed in an insulated container, and shipped to Woods Hole, Massachusetts. Panels were subsequently maintained in flowing, coarsely filtered (100 μm) sea water between 10–16°C and at ambient salinity of 30–32‰. Number and location of *M. cuneiformis* within each panel was documented by x-radiography. Individual *M. cuneiformis* were dissected from panels and maintained as above. Spontaneous spawning of gravid adults commenced upon dissection from the wood or was initiated in isolated individuals by thermal stimulation at 30°C for one hour in static, 1 μm filtered sea water at 30–32‰ salinity.

Eggs were collected and rinsed on a 20 μm "Nitex" nylon mesh, and fertilization subsequently effected in 3 l glass jars at a density of 50 eggs/ml of 0.45 μm filtered sea water equilibrated to 22 ± 2°C. Trochophore and subsequent shelled larvae were cultured in a 50 l cylindrical polyethylene (Nalgene) container at a density of 1–10/ml (decreasing from the highest density at early stages to lowest density prior to metamorphosis). Water was changed every two days at which time the larvae were siphoned on to a suitable size "Nitex" mesh and rinsed with filtered sea water. The culture container was thoroughly washed, refilled with filtered sea water, supplied with the flagellate *Isochrysis* aff. *galbana* (clone T-ISO) to a concentration of 5×10^4 cells of food per ml of final culture volume, and larvae returned to the container.

The culture was provided with continuous gentle aeration. At each water change a subsample of larvae was removed, fixed in 10% buffered formalin, and subsequently used to assay growth of the cultured larvae. This was recorded as length (anterior-posterior axis) and height (dorsal-ventral axis) on a minimum of 20 individuals from each sequential sampling. All measurements were made with a Leitz compound microscope fitted with an ocular micrometer.

All measurements of larval respiration and biochemical composition were made on larvae from one culture. Larval respiration was assayed using the differential respirometer of Grunbaum *et al.* (1955). Respirometer flasks had a volume of about 5 ml. Assays used between 100 and 1000 larva, decreasing in number with increasing size of the larvae, held in 2 ml of 0.45 μm filtered sea water in the respirometer flask. All assays were made in the absence of food organisms. Manometric readings were made at 30 minute intervals for periods of up to four hours on any one group of larvae. Computations of respiration rate used only initial and final readings. On completion of an assay larvae were fixed in 10% buffered formalin to await length and weight measurement as described earlier. Blank assays without larvae provided a control for bacterial respiration.

On each of days 15 and 35 after fertilization two extra subsamples of larvae were taken. One subsample was quickly rinsed in 3% w/v ammonium formate, washed into a clean glass vial, deep frozen, freeze dried, and subsequently stored in a sealed vial in a dessicator to await analysis. The second subsample of larvae was starved in 0.22 μm filtered sea water, under otherwise identical conditions to the actively growing larvae, for a period of three days, and then prepared for biochemical analysis as described earlier. The analytical procedures used were as follows:

(i) Individual mean dry weights were determined from weights of a known number of freeze dried larvae using a Perkin Elmer microgram balance.

(ii) Ash weight was determined from weight of the above after ignition to constant weight at 450°C. Ash-free dry weight is the difference between dry weight and ash weight.

(iii) Carbon and nitrogen contents were determined using a Perkin Elmer Carbon-Hydrogen-Nitrogen (CHN) elemental analyzer. Protein is expressed as nitrogen $\times$ 6.25.

(iv) Carbohydrate and lipid contents were determined on homogenates of known weights of freeze dried larvae in distilled water. Homogenates were prepared using a Branson sonifier. Lipid assay used a first extraction in 1:2 v/v chloroform: methanol (Bligh and Dyer, 1959), a second extraction in 2:1 v/v chloroform: methanol (Folch *et al.*, 1957), purification with 0.7% w/v sodium chloride (Marsh and Weinstein, 1966), drying of the chloroform layer, and gravimetric analysis. Carbohydrate assay used 5% cold trichloroacetic acid to precipitate protein and nucleic acids from the initial water homogenate (Holland and Gabbott, 1971). Carbohydrate content of supernatant was assayed by the phenol-sulphuric acid method of Raymont *et al.* (1963) using glucose as a standard. Reported values are mean values of triplicate analyses.

Estimates of caloric content were made from biochemical composition using the following conversion factors: protein (nitrogen $\times$ 6.25) 5.7 cal/mg, carbohydrate 4.2 cal/mg, and lipid 9.5 cal/mg (Ansell, 1972).

All measurements of respiration and excretion by adult *Martesia cuneiformis* were made on individuals dissected from the wood. Oxygen consumption was measured using a Gilson differential respirometer. During assay *M. cuneiformis* were held in filtered sea water. Pumping of water by the animals made agitation of the respirometer flasks unnecessary. Concurrent measurements were made, at the beginning and end of the assay period, of ammonia and dissolved primary amine concentration in the water containing the individual *M. cuneiformis* using the phenol hypochlorite method of Solorzano (1969) and the fluorescamine method of Undenfriend *et al.* (1972) as modified by North (1975) respectively. A minimum of two respirometer flasks containing filtered water only were included in each experimental assay to provide blank measurements of ammonia and primary amine concentrations. The fluorescamine method was calibrated against glycine. All measurements on adult animals were made within seven days of their being dissected from the collecting panel.

Results

Larval settlement is expressed as individual larvae per square meter of surface area of the wooden substrates. No settlement was recorded during January, February, and March. Settlement occurred at densities of 3.6 ind./sq. m during June and July, 151.5 ind./sq. m during August, September, and October, and 45.1 ind./sq. m during November and December.

From a total of 120 panels examined 73% of the larvae metamorphosed on the cut end grain of the wood panels, 18% on the edges and 9% on the relatively smooth, flat sides of the panels.

Upon removal from the wood, shell length, defined as the maximum anterior-posterior dimension of the valves, was recorded. Estimates of daily increment of shell length were made. These varied from 0.04–0.19 mm/day during the months of August, September, and October to 0.01–0.03 mm/day during December, January, and Feb-

ruary respectively. These are probably underestimates of the actual growth rate since they are based on the assumption that larval settlement occurred on day one of substrate immersion.

Fifty individuals were dissected from fir panels that had been immersed in sea water from 30/6/80 to 24/10/80 (116 days). These varied in length from 5 to 22 mm with a mean value of 11.7 mm. Twenty four of these individuals spawned, fourteen as males (length range 5–19 mm, mean 11.9 mm), nine as females (length range 10–16 mm, mean 11.7 mm), and one individual, of length 16 mm, as a male on one occasion and twice within the following four days as a female. Spawning activity was not related to development of the callum in that one individual with no callum spawned as a female upon removal from the wood, and a further seven individuals with no or only a partly developed callum simultaneously spawned as males. Neither was there a strong relationship between shell length and the state of development of the callum in collected specimens. Individuals with no or only a partly developed callum varied in length from 5 to 19 mm (mean = 10.3, n = 25) whereas those with a full callum varied in length from 7 to 22 mm (mean = 13.1, n = 25). No mortalities were observed as a direct consequence of dissection from the wood. Isolated pholads were maintained in flowing sea water (12–18°C) for over one year and retained the ability to spawn upon stimulation.

The first shelled veliger larva has dimensions of 69.0 ± 2.8 μm S.D. length and 60.0 ± 3.0 μm S.D. height (n = 20). From 12 to 25 days post fertilization the larva

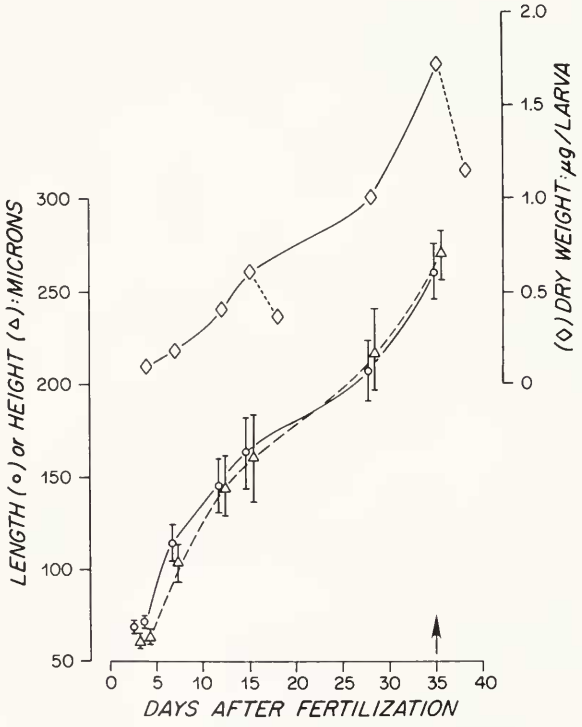

FIGURE 1. Change in length (○ —— ○), height (△ —— △) and dry weight inclusive of shell (◇ —— ◇) of *Martesia cuneiformis* throughout larval development at 22°C on a diet of *Isochrysis* aff. *galbana* (clone T-ISO). Weight loss during starvation indicated thus (◇ - - - ◇). Error bars, where given, are ±1 S.D., n = 20. Arrow on x axis indicates 50% of population are pediveliger larvae.

is approximately isodiametric (Fig. 1). The pediveliger larval foot appears at a mean shell length of 260 μm. Approximately 50% of the population reach pediveliger stage 35 days after fertilization. The dry weight (including shell) of the larva increases steadily from a mean value of 0.1 μg at 4 days post fertilization to 1.72 μg at 35 days post fertilization. Marked decreases in dry weight resulted from three day starvation periods that began on days 15 and 35 respectively (Fig. 1).

Oxygen consumption rate per larva increased allometrically with dry weight of the larva including shell (Fig. 2). The relationship is described by the equation:

$$R = 2.22W^{2.42}$$

where R is the respiration rate (nl O_2/larva/h) and W is the dry weight including shell (μg).

Marked decreases in ash free dry weight were observed during starvation (Table I). Starvation losses in a three day period amounted to approximately two thirds of the prestarvation protein and lipid contents by weight, and over three quarters of the prestarvation carbohydrate content by weight. Although absolute losses by weight were consistently highest in the protein fraction and lowest in the carbohydrate fraction the relative contributions of these fractions to energy expenditure are best examined in terms of caloric equivalents (Table I). Protein was the major contributor to energy expenditure during starvation accounting for 56 and 54% of total caloric losses during

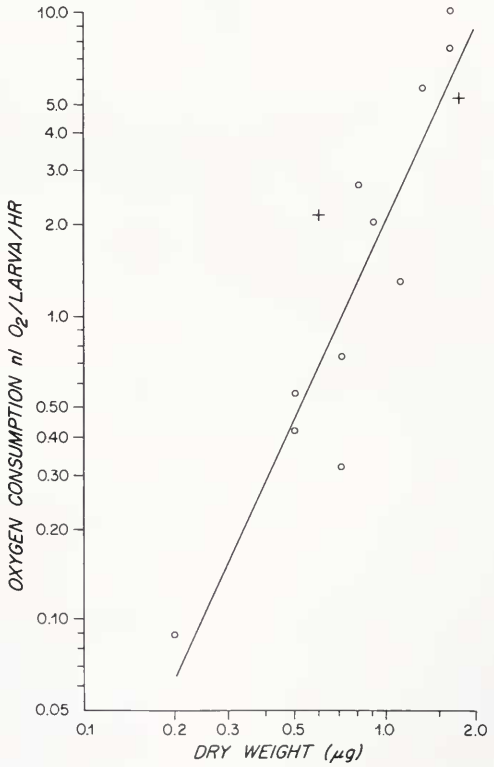

FIGURE 2. Double logarithmic plots of respiration rate and dry weight inclusive of shell for larval *Martesia cuneiformis*. Line fitted to recorded values (○): $R = 2.22W^{2.42}$, $r = 0.928$, $n = 11$, $P < 0.01$. Values recorded (+) are calculated from caloric loss during starvation (see Table I).

TABLE I

Biochemical composition of Martesia cuneiformis *larvae grown at 22 ± 2°C and 30–32‰ salinity on a diet of* Isochrysis *aff.* galbana *(clone T-ISO)*

Days after fertilization	15	18	35	38
Days fed	15	15	35	35
Days starved	0	3	0	3
Length μm	162.6		260.4	
Height μm	160.8		269.4	
Dry wt: μg/larva	0.60	0.36	1.72	1.14
Ash free dry weight: μg/larva	0.308	0.087	0.946	0.463
Biochemical content: μg/mg dry wt				
carbohydrate	10.71	3.53	25.5	8.00
lipid	80.0	47.0	59.0	30.1
nitrogen × 6.25	172.5	94.3	293.7	162.5
carbon	205.0	174.0	260.0	188.0
Biochemical content: ng/larva				
carbohydrate	6.43	1.27	43.86	9.12
lipid	48.00	16.92	101.48	34.20
nitrogen × 6.25	103.5	33.9	505.2	185.2
carbon	16.6	62.6	214.3	80.8
Biochemical content: relative contribution as calories × 10^{-6}/larva				
carbohydrate	27.0	5.3	184.2	38.3
lipid	456.0	167.7	964.0	324.9
nitrogen × 6.25	589.9	193.2	1375.4	460.6
total	1072.9	359.2	2523.6	823.8

starvation regimes initiated on days 15 and 35 respectively. By comparison lipid and carbohydrate contributed 40 and 3% of total energy expenditure respectively during the starvation regime initiated on day 15, and 38 and 9% of total energy expenditure respectively for the regime initiated on day 35.

Oxygen consumption rate increased allometrically with increasing weight in adult *Martesia cuneiformis* (Fig. 3) and is described by the relationship:

$$R = 17.95W^{0.703}$$

where R is the respiration rate (μl O_2/individual/h) and W is the live weight (grams). Ammonia excretion rate also increased allometrically with increasing weight (Fig. 3) according to the relationship.

$$E = 0.133W^{0.492}$$

where E is the excretion rate (μg at NH_3-N/individual/h) and W is the live weight (grams). Fifteen measurements of excretion of amine nitrogen were made. Results indicated a consistently low excretion rate with amine nitrogen contributing a mean of 2.8% of the total nitrogen excreted.

The ratio of oxygen consumption to total nitrogen excretion on individual assays varied between 6.8 and 24.4 with a mean value of 12.1. Despite the differences in the exponent values of the allometric relationships for excretion and respiration rates *versus* weight the O:N ratio did not appear to be closely related to the weight of the animal.

DISCUSSION

Martesia cuneiformis is a hermaphrodite possibly maturing protandrically initially as a male and subsequently as a female. A similar observation has been recorded by

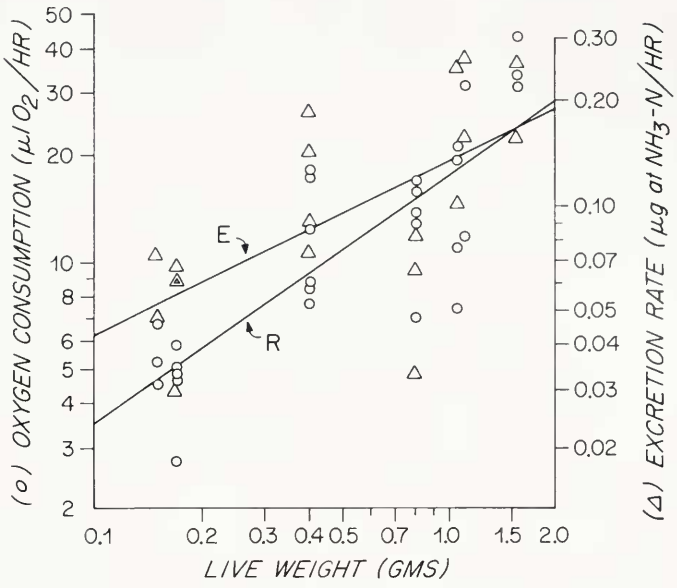

FIGURE 3. Double logarithmic plots of respiration rate (O) and ammonia excretion rate (Δ) *versus* live weight for individual adult *Martesia cuneiformis*. R = $17.95W^{0.703}$ (r = 0.827, n = 29, $P < 0.01$); E = $0.133W^{0.492}$ (r = 0.645, n = 19, $P < 0.01$).

Srinivasan and Krishnaswamy (1964) for *Martesia fragilis*. The gonad of *M. cuneiformis* can develop rapidly as the functional foot degenerates and spawning can occur prior to the development of a complete callum.

The major peak of larval settlement in the Beaufort, North Carolina area apparently occurs during late summer and early fall. No comparable data could be found on this or similar pholad species; however, this data is in contrast to that for larval settlement of the Teredinid *Bankia gouldi* Bartsch which peaks in late spring and early summer at the same location (Mann and Gallager, unpubl.). The greatest larval settlement density of 151.5 individuals/sq. m for *Martesia cuneiformis*, is also substantially lower than that of *B. gouldi* (*i.e.*, 8500 ind./sq. m in June; Mann and Gallager, unpubl.). A lower fecundity in *M. cuneiformis* and crowding of the substrates by late summer may be controlling factors of competition for space.

The maximum shell growth of 5.7 mm/month for *Martesia cuneiformis* is typical for this species with *Martesia striata* growing slightly faster at similar temperatures (Turner, per. comm.).

Spawning of gravid *Martesia cuneiformis* in the laboratory was observed only in response to physical disturbance during dissection from the wood or after thermal stimulation. This is unlike *Martesia striata* which spawns spontaneously at 21°C (Boyle and Turner, 1976). The first shelled veliger of *M. striata* is, at 68.0 μm long and 59.1 μm in height, of similar size to the first shelled veliger of *M. cuneiformis*. The pediveliger of *M. striata* at 235.7 μm long and 236.2 μm in height, is, however, smaller than that of *M. cuneiformis*. Boyle and Turner (1976) describe a tooth on one valve and a corresponding notch on the other along the ventral margin of *M. striata* pediveligers. This morphological feature does not exist in *M. cuneiformis*. Growth rate of *M. cuneiformis* larvae at 22°C is comparable to that of *M. striata* at 26°C (Fig. 1, and Boyle and Turner, 1976) but slower than reported for *Teredo navalis* Linné (Gallager and Mann, 1981a), *Crassostrea virginica* Gmelin (Dupuy *et*

al., 1978), *Ostrea edulis* Linné (Walne, 1965), or *Mytilus edulis* Linné (Bayne, 1976) under comparable conditions of temperature, salinity, and food concentration.

The respiration rate of *Martesia cuneiformis* larvae is notably lower than those reported previously for *Crassostrea virginica* by MacInnes and Thurberg (1973). The exponent value 2.42 relating weight to oxygen consumption is considerably higher than the value of 0.902 recorded for *Mytilus edulis* veligers by Riisgard *et al.* (1981), and higher than values suggested by Zeuthen (1953) for small marine organisms.

During starvation of *Martesia cuneiformis* larvae energetic losses are greatest in the protein component with a significant loss also being recorded in the lipid component (Table I). In contrast Holland and Spencer (1973) working with *Ostrea edulis,* and Gallager and Mann (1981a) working with *Teredo navalis,* both emphasize the importance of neutral lipid as the predominant energy reserve during enforced starvation of the larval stages. In general, close agreement exists between the composition data on a μg/mg dry weight basis for the larvae of *M. cuneiformis* (Table I) with those of *Ostrea edulis* of comparable size (Holland and Spencer, 1973).

The measurement of both respiration rate and change in biochemical content during starvation of *Martesia cuneiformis* larvae allows comparison of observed oxygen consumption with that calculated from oxycaloric equivalents. Calculated caloric losses during three day starvation periods initiated on days 15 and 35 respectively are 713.7×10^{-6} and 1699.8×10^{-6} cal/larva respectively (Table I), or 9.91×10^{-6} and 23.61×10^{-6} cal/larva/h respectively assuming a constant rate of depletion of reserves over the three day period. Oxygen consumption rates of 15 and 35 day old larvae are 0.64 nl/larva/h and 8.25 nl/larva/h respectively. These values give calculated oxycaloric equivalents of 15.48 cal/ml O_2 and 2.86 cal/ml O_2 respectively. When compared with respiration values calculated from biochemical component loss (Table I) and oxycaloric equivalents for individual components of 4.94 cal/ml O_2 for carbohydrate, 4.59 cal/ml O_2 for lipid, and 4.48 cal/ml O_2 for protein degraded to ammonia (values recalculated from Elliot and Davison, 1975) the recorded values suggest under and over estimation of oxygen consumption for *M. cuneiformis* larvae of 162.6 and 260.4 μm length respectively from the fitted line in Figure 2. Such an error in estimation could result from a combination of high exponent value and a low intercept value. For comparison purposes respiration rate measurements estimated from caloric losses, that is 2.16 nl/larva/h and 5.18 nl/larva/h respectively, are plotted on Figure 2.

A good agreement is noted in the exponent value of 0.703 relating wet weight to respiration rate for adult *Martesia cuneiformis* with exponent values of 0.68 for *Teredo navalis* at 21°C (Soldatova, 1961a, b), 0.76 for *Lyrodus pedicellatus* Quatrefages at 20°C (Gallager *et al.*, 1981b), 0.78 for *Mytilus edulis* at 20°C (Gallager *et al.*, 1981b), and 0.611 for *M. edulis* at 15°C (Bayne and Scullard, 1977). Definitive comparisons of absolute respiration rate are not possible because no measurements were made of dry tissue weight of the individual *M. cuneiformis.* Previously Gallager and Mann (1981b, Table III) have shown that dry tissue weight varies between 7.48 and 8.67% of the live weight of fed *Tapes japonica* (Deshayes) in the size range 1.25–1.73 g live weight. If a mean of the values calculated from Gallager and Mann (1981b) is applied to *M. cuneiformis* the relationship plotted in Figure 3 becomes:

$$R \text{ (ml } O_2\text{/individual/h)} = 0.264W^{0.703}$$

where W is the dry tissue weight in grams. While the validity of this estimate is limited by the application of data from *T. japonica* to *M. cuneiformis* it is notable that the value of the constant obtained, that is 0.264, is comparable to those recorded for the byssaly attached *Mytilus edulis* (0.302 and 0.398 by Bayne and Scullard, 1977; and

Gallager *et al.*, 1981b respectively) but considerably lower than those recorded for actively boring teredinids (1.20 by Soldatova, 1961a, b; and 1.313 by Gallager *et al.*, 1981b). Gallager *et al.* (1981a) previously showed that respiration rate increases approximately four fold on transition from quiescence to active boring in the teredinid *Bankia gouldi*. It is probable that similar increases occur in adult *M. cuneiformis* during active boring in a wood substrate.

The exponent value of 0.492 which relates ammonia excretion rate to wet weight of individual adult *Martesia cuneiformis* is lower than the corresponding exponent for respiration. Bayne (1976, Table 6.5) summarizes data on seasonal changes in the exponent for excretion rate in *Mytilus edulis* and shows it to vary between 0.35 (starved animals in winter) and 1.20 (fed animals in winter). The value recorded in the present study is comparable to those recorded by Mann (1979a) for *Crassostrea gigas* at 12–18°C and *Ostrea edulis* at 12–15°C. The low contribution of amine nitrogen to the total excreted nitrogen is not typical of other reports in the literature. Hammen (1968) reported contributions of amine nitrogen to the total excreted by *Tagelus plebius* that varied from 31% (normal) to 67% (stressed animals). Similarly Bayne (1973) found that the proportion of amino nitrogen excreted increased from 55 to >75% during temperature and starvation stress in *M. edulis*. Recent criticism of the fluorescamine technique suggests that comparison of the present data with literature values obtained by other methods is difficult. Wright (1982) states that fluorescamine may react with primary amines other than amino acids; *e.g.*, ammonia, thus introducing an overestimation of the contribution of amines to total nitrogenous excretion; however, even if this overestimation was made in the present study the observation concerning proportionately low amino acid excretion in *M. cuneiformis* still remains valid.

The significance of the ratio of oxygen consumption to ammonia excretion as an indicator of predominant respiratory substrate in marine bivalves has been discussed at length in Bayne (1976, pp. 268–270). The values recorded for *M. cuneiformis* are low and indicate a strong dependence on protein. Biochemical component assays of adult animals were not made to substantiate this conclusion; however, the individual animals on which O:N ratios were recorded had well developed callums, were reproductively active or both. Gametogenesis often proceeds at the expense of stored lipid and carbohydrate reserves in marine molluscs (see Gabbott 1975, Mann 1979a, b) and the post-spawning period is often marked by a notable increase in ammonia excretion rate as protein reserves are utilized more intensively (Mann, 1979a, b). It is not, therefore, unreasonable to suggest that the low O:N ratio recorded here is a result of prolonged spawning activity and depletion of reserves.

Acknowledgments

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